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Learning to adapt: Dynamics of readaptation to geometrical distortions

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ABSTRACT

The visual system can adapt to optical blur, whereby the adapted image is perceived as sharp. Here we show that adaptation reduces blur-induced biases in shape perception, with repeated adaptations (perceptual learning), leading to unbiased perception upon re-exposure to blur. Observers wore a cylindrical lens of +1.00 D on one eye, thus simulating monocular astigmatism. The other eye was either masked with a translucent blurred lens (monocular) or unmasked (dichoptic). Adaptation was tested in several repeated sessions with a proximity-grouping task, using horizontally or vertically arranged dot-arrays, without feedback, before, after, and throughout the adaptation period. A robust bias in global-orientation judgment was observed with the lens, in accordance with the blur axes. After the observer wore the lens for 2 h, there was no significant change in the bias, but after 4 h, the monocular condition, but not the dichoptic, resulted in reduced bias. The adaptation effect of the monocular 4-h adaptation was preserved, and even improved, when the lens was re-applied the next day, indicating learning. After-effects were observed under all experimental conditions except for the 4-h monocular condition, where learning took place. We suggest that, with long experience, adaptation is transferred to a long-term memory that can be instantly engaged when blur is re-applied, or disengaged when blur is removed, thus leaving no after-effects. The comparison between the monocular and dichoptic conditions indicates a binocular cortical site of plasticity.

1. Introduction

Evidence for plasticity in the adult visual system has been reported in human studies of perceptual learning, which have demonstrated that training for specific visual tasks leads to long-term improvement in performing the task (Fahle, 2002). Adaptation is a widespread phenomenon in the visual system, occurring on multiple time-scales, ranging from seconds to hours, according to the type of the change involved and its duration (Kohn, 2007; Kwon, Legge, Fang, Cheong, & He, 2009). One intensively studied form of adaptation is adaptation to contrast. Adaptation with a high-contrast stimulus causes a reduction in contrast sensitivity of a test stimulus (Blakemore & Campbell, 1969; Graham, 1989). Both orientation specificity and interocular transfer suggest a cortical locus for the perceptual effect because orientation tuning and binocular responses first occur in V1 (Kohn, 2007; Kwon et al., 2009). Thus, unlike light adaptation, contrast adaptation involves effects both in the retina and in the cortex. Perceptual after-effects show similar specificity for simple stimulus attributes such as orientation and spatial and temporal frequency, but also for stimulus correlations or conjunctions. For example, in the McCollough effect, adaptation to pairs of colored gratings causes colorless test gratings to appear tinged with the opposite color to the similarly oriented component of the adapter (McCollough, 1965). Another type of adaptation, the tilt adaptation, transfers between eyes: the illusory rotation is seen even when the tilt adapting grating is presented to one eye and the test grating to the other eye. However, the amount of apparent rotation is greater when the adapting and the test stimuli are presented to the same eye and the transfer from one eye to the other is only partial (Mitchell, 1980). In prism adaptation subjects are able to adapt to geometric distortions in the visual field that are caused by prism goggles, such as when reversing the visual input upside-down (Gonshor & Jones, 1976).

So far there is no evidence for a common mechanism underlying adaptation and perceptual learning (Harris, 1980) and for the exact conditions that are needed to induce these effects, as well as the different temporal properties of the neuronal processes underlying these two phenomena. Here we investigated whether adaptation is affected by previous experience with the adapting stimulus. Can adaptation become more effective with experience? Efficient adaptation processes may reduce biases in perception, both when the adapting stimulus is applied and removed, the latter by reducing the duration of after-effects. Adaptation differs from perceptual learning in being typically temporary, depending on the presence of the adapting stimulus. It is induced by exposure to the stimulus per se rather than by task-specific practice, whereas the effect of perceptual learning depends on the task and persists for months and

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years without exposure to the learned task (Ball & Sekuler, 1987; Fahle, 2002; Fiorentini & Berardi, 1981; Gibson, 1969; Karni & Sagi, 1991; Sagi & Tanne, 1994). Moreover, adaptation was shown to depend on the number of interactions between the visual and motor systems via feedback that was provided to the observers, and not on the time spent wearing the distortion (e.g., Harris, 1980), whereas no after-effect developed in the absence of visuo-motor interaction (Fogt, 2000; Held, 1965). It has been suggested that the functional role of adaptation is to provide flexibility to function under varying external conditions (Schwabe & Obermayer, 2002).

Previous studies have demonstrated visual adaptation to a perceived distortion (or blur), that is, the visual system adjusts to image blur so that blurred objects look sharp (Webster, Georgeson, & Webster, 2002). Furthermore, adaptation to blur was found to improve visual resolution (Pesudovs & Brennan, 1993). It was also suggested that the neural visual system is adapted to the eye's aberrations, thereby removing the effects of blur generated by the sensory apparatus from visual experience (Artal et al., 2004). In this work we studied how adaptation affected blur-dependent global shape perception and its long-term retention. To achieve this goal, we induced an artificial one-dimensional visual blur by using a cylindrical lens of 1D mounted in front of one eye of the observers, and probed the underlying mechanism and the time-course of the adaptation effect. Such a lens is expected to have two main effects on the retinal image along the lens axis: blur and magnification, with the latter being relatively small here (see Appendix A). We used the Gestalt grouping task where an image, consisting of numerous discrete elements, generates a perception of a global form governed by some simple rules. These rules rely on basic image properties such as the elements' proximity, similarity, continuity, common fate, and closure (Koffka, 1935). The application of directional blur to such a pattern elongates the local elements and thus is expected to bias perception toward the direction of the blur. This paradigm combines an induced optical distortion with a global visual task. Whether adaptation to blur eliminates this bias is not clear, since it is possible that adaptation to blur does not affect the integrative processes underlying grouping. To quantify the blur-induced bias, we manipulated the distance between image elements in order to counteract the blur-induced grouping by proximity grouping. The proximity bias required to balance the blur effect was used as a measure of blur bias, allowing us to trace changes through the adaptation period and the effects due to repeated adaptations. This bias was shown to depend on spatial integration over many image elements, pointing to global effects (Ben-Av & Sagi, 1995). Our results show that adaptation to blur eliminates blur-induced biases in global shape perception, and, more importantly, that adaptation to blur is preserved between repetitions, in the absence of the inducing blur, thus indicating changes in long-term memory and learning.

2. Methods

2.1. Observers

Thirteen naive observers participated in the experiments. All were high-school or undergraduate students (ages ranged from 17 to 32), with normal or corrected-to-normal visual acuity (see Table 1 for the refractive state), and who were unaware of the purpose of the study. Each observer signed an informed consent form approved by the local Institutional Review Board of Sheba Medical Center.

2.2. Apparatus

The experiments were controlled by a PC and the stimuli were displayed as a gray-level modulation on a Philips 107P color monitor. The mean display luminance was 20 cd/m^2 in an otherwise dark environment. Screen resolution was 1024 × 768 pixels; gamma correction was applied. The stimuli were viewed from a distance of 150 cm.

Table 1
Refractive state. The refractive state for each subject was measured before the experiment. The experiment was performed using a full optic correction.

Name	Right eye	Left eye
KS	−3.75	−3.00
CY	Plan-0.50 × 150	+0.50–0.50 × 160
GS	+0.50	+0.50
IS	−2.00	−1.75–0.75 × 135
KaS	−3.00	−2.75–0.25 × 30
MH	+0.50–0.25 × 175	+0.25–0.25 × 170
GF	−3.50	−3.25–0.50 × 170
MZ	−2.50–0.50 × 95	−2.50–0.25 × 105
OY	−2.00–0.50 × 90	−2.00–0.50 × 90
AS	+0.25	+0.25
EV	+0.25–0.50 × 150	+0.25–0.50 × 35
TL	−0.50–0.25 × 100	−0.25–0.25 × 80
RK	+0.50–0.25 × 180	+0.25–0.25 × 180

2.3. Stimuli

A matrix of white dots was presented on a gray background; each dot diameter was 6 pixels (Fig. 1). The dot size was 2.5 min of arc. The dot intensity was 45 cd/m^2. By adding a cylindrical lens, we changed the viewer's perception. The dots were elongated toward the more blurred meridian, resulting in a bias toward the more cylindrical meridian. The experimental variable was the vertical and the horizontal relative distance (d_h/d_v) between the centers of the dots. According to the law of proximity, when a dot matrix is presented with a different gap size in the horizontal or vertical direction, the dots tend to be perceptually grouped by proximity, in such a way that the matrix can be perceived as columns, rows, or as an ambiguous pattern. The distance between the dots was changed over the vertical or horizontal direction; the 7 d_h/d_v ratios tested were 1.33, 1.21, 1.1, 1, 0.9, 0.82, and 0.75 (the higher ratio is normally perceived as columns). The spacing between the dots within the dot-array was 33.75 min of arc for a d_h/d_v ratio of 1, which means equal distances. The lens also induced a minor magnification of 1.2%.

The appearance of the margins of the matrix was under most of the conditions rectangular, due to the unequal spacing between the rows and columns, which may have interfered with the observers' judgment. To avoid such interference, the screen was covered with a round window with a radius of 5 cm, so that the global form of the stimulus was circular across all experiments, occupying 3.8 deg of the visual field (Fig. 1).

2.4. Visual task

The task was to report the perceptual organization of the display as horizontal rows or vertical columns, with no feedback. The measures were obtained for each eye, separately, before, during, and after the adaptation period. A cylindrical lens of +1.00 Diopter at the 90 meridian was mounted 12 mm in front of the dominant eye (vertex distance) in order to create an optical blur (*+1.00/−1.00 D × 90*). Once a cylindrical lens is mounted, a one-dimensional blur along one meridian is created, according to the cylindrical axis. As a result, immediately after mounting, a round dot is perceived as an ellipse, which can promote grouping along a specific orientation. Thus, this can provide an additional cue for grouping, along with the change in the proximity between the dots

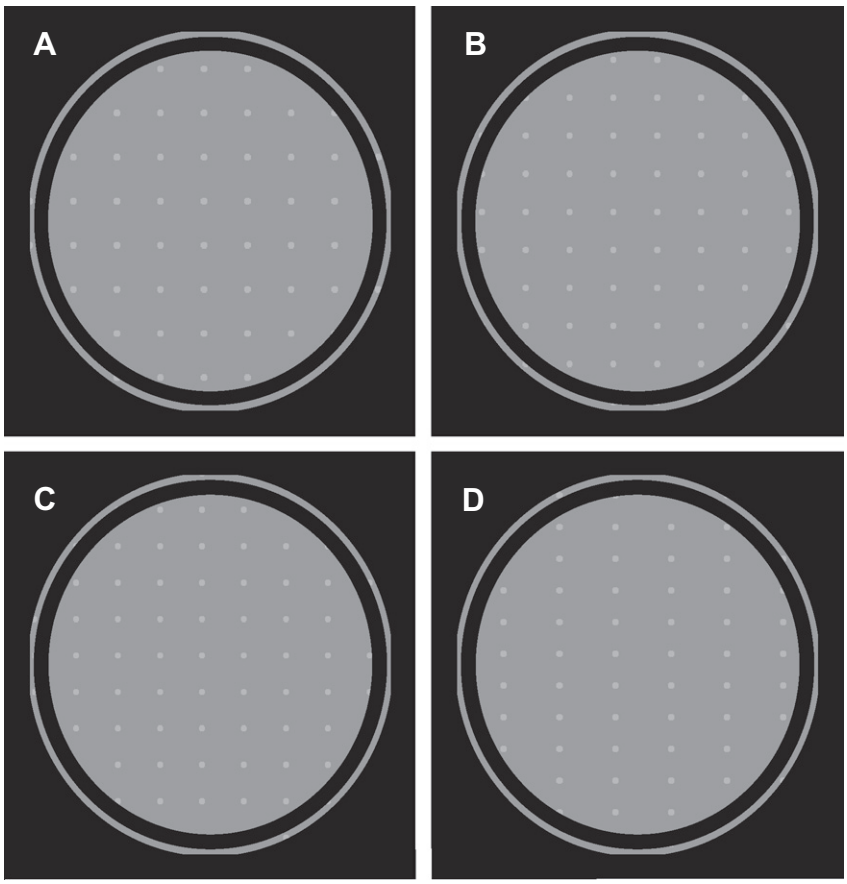

Fig. 1. The stimuli. The experimental variable is the relative ratio of the horizontal and the vertical distances (d_h/d_v) between the dots in the matrix. The ratio could be (A) equal, i.e., $d_h/d_v = 1$, or d_h/d_v could change to (B) 10%, (C) 20%, and (D) 30% in either the vertical or the horizontal direction.

along one axis – the combination of the two determines the grouping (Kubovy, Holcombe, & Wagemans, 1998).

The observers wore the cylindrical lens for an adaptation period of either 2 or 4 h during each session. During the adaptation period, the observers were tested every 2 h. The unadapting eye was either covered with a translucent blurred lens (monocular group) or was left open (dichoptic group). Thus, four groups of observers were tested (2 adaptation periods $\times$ 2 viewing conditions). During the adaptation period, the observers were instructed to be active and to perform any type of visual tasks. The observers were tested again before removing the lens and immediately after. The other eye was tested (separately) at the baseline and after removing the lens.

Data were collected in seven blocks of 40 trials. Each block contained all seven different d_h/d_v ratios, intermixed, which resulted in a run of 280 trials that lasted between 8 and 15 min. Each trial was preceded by a fixation mark at the center of the display until the observer signaled his readiness using the computer mouse. Then a stimulus was briefly presented for 80 ms. The observer responded by pressing the mouse buttons: right for vertical grouping (columns) and left for horizontal grouping (rows).

Each observer repeated the adaptation session until saturation, up to four sessions (2.4 sessions on the average), on different days, within a period of 10 days. Four or five measurements were taken in each session: before wearing the lens (baseline), immediately after wearing the lens (t_0), after a 2-h and 4-h adaptation with the lens (t_2 and t_4), and immediately after removing the lens (post-test).

2.5. Fitting

The data were fitted using the following equation:

$$f(x) = 2^{-(x/b)^p} \quad (1)$$

where $x > 0$ is the ratio between the displayed horizontal and vertical spacings (d_h/d_v), f is the percentage of "horizontal" report, b is the perceived equilibrium (PE) point in vertical/horizontal judgment, and p reflects the steepness of the psychometric curve. For all fits $r^2 > 0.95$.

2.6. Data analysis

We used a paired two-tailed t-test for comparing conditions in order to estimate the adaptation effect.

3. Results

Perceptual grouping is used to determine whether the spatial arrangement of a dot matrix is perceived as columns or rows. A psychometric curve was obtained for each observer and then the average for the group was calculated (Fig. 2). The percentage of horizontal judgments (reported as rows) is plotted separately for each relative spacing (d_h/d_v) between the dots. In baseline measurements that were carried out before adapting to the induced blur, the observers displayed no perceptual bias: they accurately judged the stimulus organization, with a sharp transition between the vertical and horizontal perceptions. When d_h/d_v was less than 1, the dots were perceptually grouped into rows, whereas when d_h/d_v was more than 1, the dots were perceived as columns. As shown in Fig. 2, the measured perceptual grouping was very accurate; when d_h/d_v differed from 1 by 10% or more, the discrimination was above 90%. However, in an ambiguous situation, when d_h/d_v

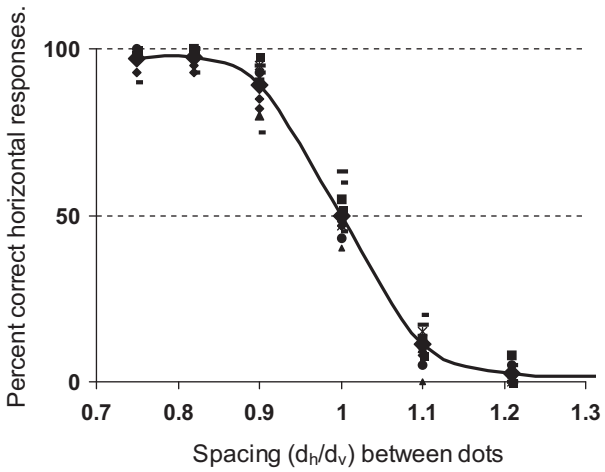

Fig. 2. Grouping task: the psychometric curve. The *X*-axis represents the relative spacing (d_h/d_v) between the dots, and the *Y*-axis represents the percentage of horizontal judgments reported. Perception follows the physical arrangement of the stimulus. Shown are results from 13 observers (different symbols) before wearing the cylinder lens.

was equal to 1 (equal spacing), the perceived arrangement of the dot matrix was almost equally distributed between vertical and horizontal.

3.1. Adaptation for 2 h

3.1.1. Monocular group

Observers wore a cylindrical lens for a period of 2 h and perceptual grouping was measured before, during, and after wearing the lens. Fig. 3A presents a 2-h session of one observer (KS). We analyzed the value of the reported equal vertical and horizontal distances ("perceived equilibrium", PE; 50% of correct answers for each direction, vertical and horizontal). Since the task included seven different ratios, we used curve fitting in order to find the ratio of the (parameter "*b*" in Eq. (1)) between the horizontal and the vertical distances. At the baseline, there was no significant perceptual bias: the ratio for which the observer KS reported equal perception was 0.993. Immediately after the observer wore the lens (t_0), the curve was shifted according to the induced blur by the toric lens, i.e., toward the vertical meridian, so that the perception of the dot matrix shifted toward the vertical columns. The PE here was 0.948 at t_0. After the lens was worn for 2 h, at t_2, the PE increased to 0.96, showing only a slight change. The bar plot in Fig. 3B presents the calculation of deviation of PE in percent throughout all the stages of the test session. In this example, at the baseline, there was no perceptual bias (0.7%). At t_0, the perceptual bias was 5.2% (PE = 0.948) in the vertical direction. After 2 h, at t_2, the perceptual bias was 4% (PE = 0.96) in the same direction. These results do not exclude the existence of adaptation operating on a time scale faster than our measurement, but rather indicate an incomplete adaptation.

Fig. 4 presents the results, relative to baseline, of five observers who were tested under the same conditions: each observer repeated the session 2–4 times, on different days. We examined the change in the perceived bias between the first time the lens was applied (i.e., t_0) and the last measurement before the lens was removed (i.e., t_2) (Fig. 4A, $N = 5$). The baseline was 0.05 ± 1.39% (mean, SE). At t_0, the perceptual bias was 5.27 ± 1.16% in the vertical direction, showing a significant perceptual bias relative to baseline ($p = 0.007$). At t_2, at the end of the experiment, the bias was 2.8 ± 1.15%, which is not significantly different from the distortion at t_0 ($p = 0.12$) but shows a barely significant difference from the baseline ($p = 0.053$). Thus, adaptation was incomplete after 2 h.

3.1.2. Dichoptic group

The above experiment was repeated with one exception: the untreated eye was uncovered during the adaptation. The results of new observers (Fig. 4B, $N = 4$) were similar to those of the monocular group. The bias at baseline was 0.65 ± 1.95%, whereas the lens induced a significant bias of 4.26 ± 1.27% at t_0 ($p = 0.02$) relative to the baseline. At t_2, the bias was 2.86 ± 0.59%, which is significantly different from that at the baseline ($p = 0.01$) but is not significantly different from t_0 ($p = 0.1$), thus showing incomplete adaptation.

3.1.3. After-effect

An after-effect was found for the treated eye in both groups, monocular and dichoptic, following the 2-h adaptation, after the toric lens was removed at the end of the last session. This after-effect reflects a perceptual bias in a direction opposite from the blur that was induced by the lens. The monocular group exhibited a sig-

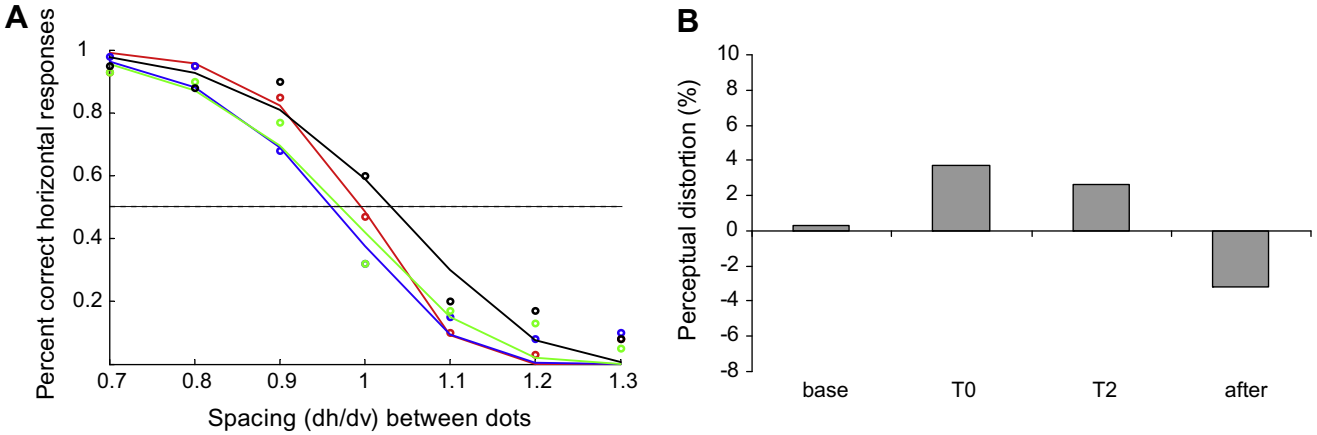

Fig. 3. Monocular 2-h adaptation experiment. A representative observer (KS). (A) The baseline psychometric curve is unbiased (red). Wearing a cylindrical lens with a vertical axis (t_0) induced a shift to the left, with a perceived equilibrium at $d_h/d_v < 1$ (blue). After the observer wore the cylindrical lens for 2 h, the distortion did not change. Removing the lens resulted in a reversed shift to the right, with a perceived equilibrium at $d_h/d_v > 1$ (black). (B) Perceptual distortion: the change in perceived equilibrium [$100(1 - b)$, b in Eq. (1)]. Positive and negative values reflect bias in the vertical and horizontal directions, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

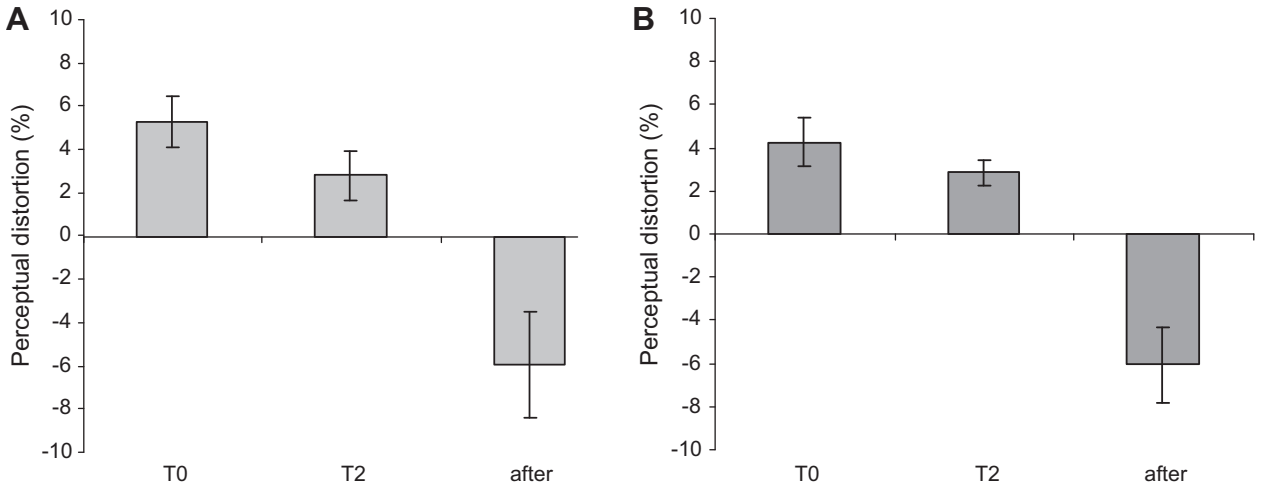

Fig. 4. Two hours of adaptation. All values are relative to the baseline. (A) Monocular group, baseline is 0.05 ± 1.39% (N = 5). (B) Dichoptic group, baseline is 0.65 ± 1.94% (N = 4). Error bars are 1 SE.

nificant (p = 0.027) after-effect of −5.92 ± 2.45%, implying a perceptual bias in the horizontal direction (Figs. 4A and 6). There was also a significant difference between the post-test and t_2 (p = 0.04). The results of the dichoptic group are similar to those of the monocular group (Figs. 4B and 6); the after-effect was significant (−6.07% ± 1.73%; p = 0.027) and the post-test was significantly different from t_2 (p = 0.004).

3.2. Adaptation for 4 h

3.2.1. Monocular group

Since 2 h were insufficient for complete adaptation, we extended the period that the cylindrical lens was worn to 4 h. This group consisted of the five observers that received the 2-h monocular adaptation, and another four naive observers (total, N = 9). Each observer repeated the session 1–3 times, on different days, within a period of 10 days. We compared the results between the first time the lens was applied (i.e., t_0) and the last measurement before the lens was removed (i.e., t_4). Fig. 5A presents the average results of the perceptual bias at t_0 and after 4 h of adaptation (t_4). At the baseline (not shown), there was no significant perceptual bias (−0.85 ± 1.03%); at t_0, the perceptual bias was 6.42 ± 2.73% (p = 0.037) relative to baseline, in accordance with the induced blur. At t_2, the bias was 5.29 ± 2.55%, which was similar to t_0 (p = 0.76), a significant perceptual bias relative to baseline (p = 0.039). However, at t_4 the perceptual bias was reduced to 1.65 ± 2.17%, relative to baseline, which was not significant (p = 0.47). This perceptual bias was significantly smaller than the one found at t_2 (p = 0.006). The reduced bias indicates that the visual system adapts to the induced bias after 4 h and that the perceived bias is significantly reduced.

3.2.2. Dichoptic group

The above 4-h experiment was repeated with one exception: the untreated eye was uncovered during the adaptation, using the same four observers of the 2-h dichoptic group. As seen in Fig. 5B, the baseline measurements showed no significant perceptual bias (0.71 ± 0.41%); at t_0, there was a bias of 6.42 ± 2.73%, showing a significant effect relative to baseline (p = 0.043). At t_2, the bias was 5.51 ± 2.27%, which was not significantly different from t_0 (p = 0.125). At t_4, the bias was 4.86 ± 2.61%, which was not significantly different from the bias at t_0 and t_2 (p = 0.2 and 0.4, respectively) and not significantly different from baseline (p = 0.060). Thus, unlike the monocular group, the perceptual bias

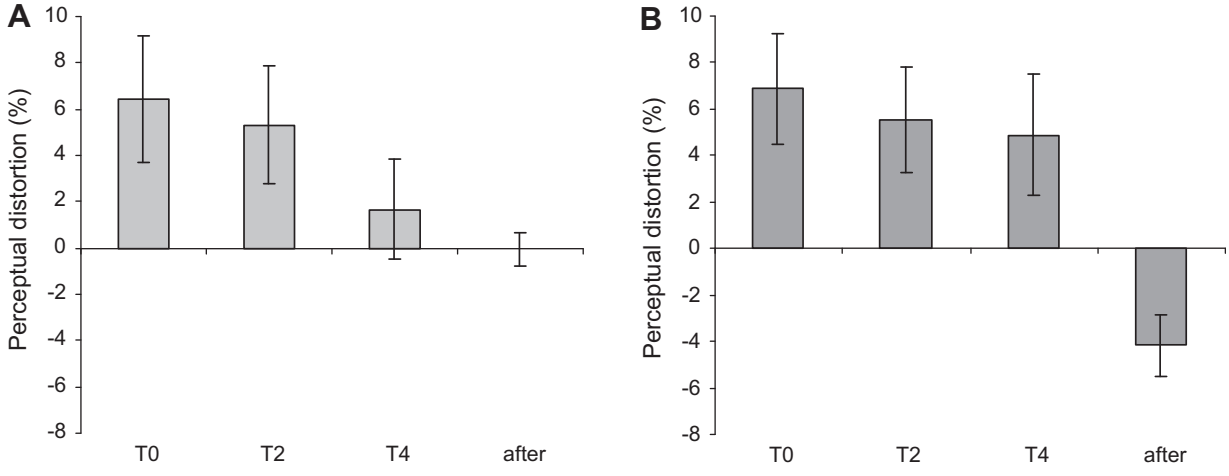

Fig. 5. Four hours of adaptation. (A) Monocular group: note the strong adaptation effect and the absence of an after-effect. All values are relative to the baseline (−0.85 ± 1.03%, N = 9). (B) Dichoptic group. All values are relative to the baseline (0.71 ± 0.41%, N = 4).

in the dichoptic group was not reduced, showing no adaptation to the blur in the visual field.

3.2.3. The after-effect

The two groups that received a 4-h adaptation showed different results for the tested eye after the lens was removed.

The monocular group exhibited the adaptation effect with no residual bias. However, the dichoptic group that did not exhibit an adaptation effect exhibited a significant after-effect in the opposite direction of the blur, induced by wearing the lens (Fig. 6).

The after-effect of the monocular group was −0.05 ± 72%, which is significantly different from t_0 and t_2 ($p < 0.05$), but is similar to the baseline ($p = 0.944$). The after-effect of the dichoptic group was −4.17 ± 1.31%, in the opposite direction to that induced by the lens. This result is significantly lower than the baseline measurement ($p = 0.035$).

3.3. Learning effect between days for the monocular group

The effect of learning was tested with four observers. A comparison of the average results between the first and the second sessions of the 4-h group revealed that the perceived bias was reduced (Fig. 7). The perceptual bias, at t_0 and t_4, decreased in the second session compared with the first one. In fact, the four measurements present a continuous decrease in bias from 5 ± 2.3% at t_0 of the first session to 0.68 ± 2% at the end (t_4) of the second session, with an intermediate bias of 3.6 ± 1.18% at the end (t_4) of the first session and bias of 2.7 ± 1.93% at the beginning (t_0) of the second session. The total reduction of the bias from t_0 in the first session to t_4 in the second was 4.31 ± 1.02% ($p = 0.016$). The bias at the end of the second session was greatly reduced relative to that of the first session (0.68% vs. 3.6%, $p = 0.047$, one tail t-test), pointing to a learning effect. This result indicates the presence of a long-term "memory" that preserves the previously corrected blur, along with the ability to re-apply the correction when the lens is applied the next day. This memory seems to be unaffected by the unbiased exposure between the sessions for adaptation, suggesting a fast consolidation (Karni & Sagi, 1993). Thus, the adaptation process that led to a decreased bias influenced the perceptual bias during the next session and, consequently, the effect of the cylindrical lens was diminished.

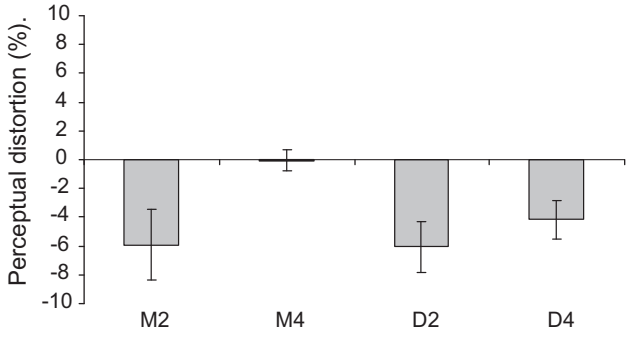

Fig. 6. The after-effect. Distortions after lens removal are shown for the dichoptic 2-h (D-2) and 4-h (D-4) groups and for the monocular 2-h (M-2) and 4-h (M-4) groups. All groups except for the monocular 4-h group exhibited a significant after-effect. Error bars are 1 SE ($N = 4$).

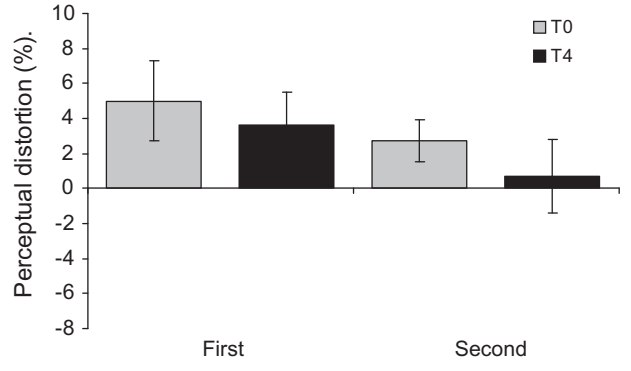

Fig. 7. Monocular 4-h group: the learning effect. A comparison of the first two sessions shows a continuous decrease in distortion across the two sessions, from 5 ± 2.3% at t_0 of the first session to 0.68 ± 2% at t_4 of the second session.

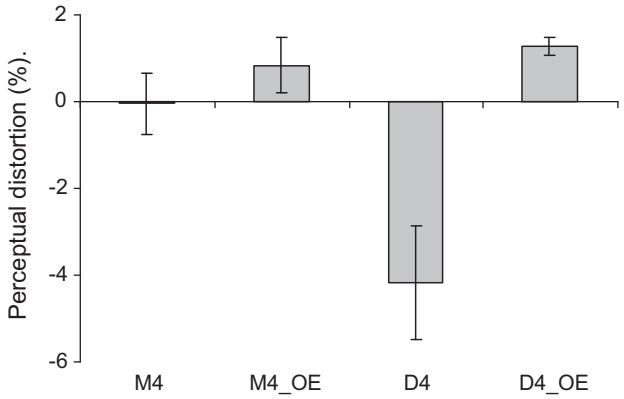

Fig. 8. The 4-h group: transfer to the un-adapted eye. After-effects at the un-adapted (M4_OE, D4_OE) eye compared with the adapted eye (M4, D4). A significant distortion of 1.26 ± 0.2% was observed for the un-adapted eye in the dichoptic group (D4_OE). Error bars are 1 SE ($N = 4$).

3.4. Transfer to the untreated eye

The untreated eye of both 4-h groups was tested in five observers before the cylindrical lens was mounted and again after it was removed, in order to examine the transfer of the adaptation effect to the untreated eye (Fig. 8). In the monocular group, after the lens was removed, the untreated eye showed no significant bias compared with that measured at the beginning of the session; the bias was 0.85 ± 0.64%, whereas the treated eye showed a bias of −0.48 ± 1.71%. In the dichoptic group, the untreated eye showed a bias of 1.26 ± 0.2% in the vertical direction, whereas the treated eye showed an after-effect of −4.17 ± 1.31%. Unlike the monocular group, the dichoptic group showed a significant perceptual effect in the untreated eye ($p = 0.001$).

4. Discussion

Our results indicate that the perceptual system fully adapts to the astigmatic lens after two 4-h adaptation periods. The effects of the two periods accumulate as in perceptual learning. A comparison of the monocular and the dichoptic groups shows a significant difference after 4 h of wearing the lens (at t_4) but not after 2 h (at t_2). Whereas the bias decreased for the monocular group, it did not significantly change for the dichoptic group, probably because of the differences in the images shown to the two eyes. A marked after-effect in the direction opposite the blur induced by the cylindrical lens was always found when no learning effect was found, whereas no after-effect was found when a learning effect was observed (monocular group 4 h). The results suggest that adaptation can be learned. Apparently, for effective learning of adaptation, adaptation periods of 2-h are not sufficient but 4 h are. Thus, the results suggest that, with long experience, adaptation is trans-

ferred to a long-term memory that can be instantly engaged when blur is re-applied, or disengaged when blur is removed, thus leaving no after-effects. The comparison between the monocular and dichoptic conditions indicates a binocular cortical site of plasticity.

4.1. Adaptation and perceptual learning

Adaptation usually differs from perceptual learning in being induced by exposure to stimuli per se rather than by task-specific practice. Moreover, the effect of adaptation is typically temporary and goes away when the cause is removed, such as in contrast adaptation (Blakemore & Campbell, 1969) or the McCollough effect (McCollough, 1965), whereas the effect of perceptual learning tends to persist over months and even years after practice (Ball & Sekuler, 1987; Fahle, 2002; Fiorentini & Berardi, 1981; Gibson, 1969; Karni & Sagi, 1991; Sagi & Tanne, 1994). This difference in effects is not so surprising since perceptual learning is thought to operate in a very specific manner, which depends on stimulus and task, whereas adaptation (as in prism adaptation or in sensory adaptation) is thought to reflect a recalibration of the visual machinery to handle a change in the visual world. Although prism adaptation may also rely on correct handling of the environment via feedback from actions taken, it is not expected to depend on specific task requirements, as perceptual learning does. Thus, the learning effect obtained here with the grouping task (following 4-h sessions) reflects learning of adaptation to the induced blur rather than of the task per se. This conclusion is motivated by the nature of the task used, i.e., perceptual grouping without feedback, which does not produce any error signal that could drive the observers' perception. This result is surprising, since it points to the possibility of storing multiple transformations of the visual world and applying them when the need arises.

In our study, we gave no feedback during the measurements, and the observers were allowed to be engaged in any kind of activity during adaptation, so they may have utilized naturally guided visual and other sensory information. However, one should note that the usual sensory activity differed from the grouping task without direct interaction between them.

One concern is that the bias observed here is due to changes in response strategy as a result of changing stimulus statistics during testing. Indeed, for un-adapted subjects, the stimuli seen through the astigmatic lens are elongated in the vertical dimension, and thus there is a higher frequency of vertical stimuli. Subjects, in situations of uncertainty concerning a stimulus orientation, may choose to follow this prior, or knowing that the stimulus is biased, act against it. Our results do not support such an interpretation since, during testing, the dichoptic condition exposes the subjects to the same stimulus statistics as the monocular condition but only the latter show the learning effect. Furthermore, decision biases estimated using methods of Signal Detection Theory converge relatively fast, within 10–20 trials (Green & Swets, 1966) while our learning effect take a few daily sessions to develop.

Another possible concern is that myopic observers can tolerate more blur because they regularly adapt to blur when they remove their glasses. However, there was no significant difference in the t_0 measurements between the myopic observers and the rest of the subjects ($p = 0.624$, two sample t-test, see Table 1), indicating that the changes in bias that the observers report do not reflect concomitant threshold changes.

4.2. After-effect

The after-effect is the response of the visual system measured after the source of the adaptation has been removed, indicating how the visual system adjusts to a continuous visual input (Mather, Verstraten, & Anstis, 1998). In our experiments, after the lens was removed, a robust after-effect in the direction opposite the induced blur was found, without a learning effect, in both the 2-h groups and the 4-h dichoptic groups. Although interesting, this effect was not found in the monocular group after the astigmatic lens had been worn for 4 h – the only group that demonstrated learning. This indicates that learning abrogated the after-effect. Thus, our results differ from the typical prism adaptation but seem to resemble the effect of prismatic adaptation induced by the optical lens (Fernandez-Ruiz & Diaz, 1999; Fogt, 2000; Tuan & Jones, 1997). In both cases, no after-effect is found when observers have learned to compensate for the visual bias, whereas an after-effect is found when this process was not completed. It was found that the after-effect is correlated with the ability of the observer to switch between two different optical corrections that induced different visual distortions: those who learned did not show an after-effect, whereas those who did not learn did show an after-effect (Fogt, 2000).

The existence of an after-effect is thought to indicate the presence of an adaptation process or a transient recalibration process. We found, with the 2-h groups, strong after-effects with little, not statistically significant, adaptation. It is possible that adaptation takes place during the few minutes (8–15) required by our measurement method to estimate the grouping bias. This is consistent with the expectation for a much larger initial bias (see Appendix A) when applying the astigmatic lens. Very importantly, the adaptation here reflects learning an alternative visual reality, which can be instantly transformed to a standard, once the lens is applied but is reversed when the lens is removed. This predicts no after-effect, which is consistent with our results when learning is found.

4.3. Accommodation

Accommodation could possibly account for the adaptation. Reduction of visual resolution immediately following defocus blur is a universal optical phenomenon (Smith, Jacobs, & Chan, 1989). Astigmatic accommodation usually has a small amplitude (<0.25 D) under monocular viewing conditions and is present only in some eyes (Byakuno, Okuyama, Tokoro, & Akizawa, 1994; Millodot & Thibault, 1985; Tsukamoto et al., 2001; Ukai & Ichihashi, 1991). The time-course of accommodation spans from a few seconds to minutes, but not hours. For example, Stark and colleagues reported the time-course of seconds in response to induced astigmatism (Stark, Strang, & Atchison, 2003). Mon-Williams and colleagues also noted a larger change in both monocular and binocular VA after a 30-min period of induced defocus in an emmetropic population (Mon-Williams, Tresilian, Strang, Kochhar, & Wann, 1998). It was suggested that the improvement in visual acuity results from perceptual adaptation to the blurred images, which may occur at central sites within the visual cortex (George & Rosenfield, 2004). Therefore, the adaptation effect that we found after 4 h but not after 2, as we showed in our study, could not be explained by accommodation.

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Appendix A

A.1. Motivation

A cylindrical lens of +1.00 D induces a complex effect – a combination of blur and magnification. Blur changes the shape of the

stimulus along the axis of the cylinder, whereas magnification expands the entire image in the same direction. We consider here possible effects on our stimuli composed of dot matrices. Blur makes the circular dot elements elliptical, with a width ratio of ~2, whereas magnification is expected to be relatively small (~1.2%) under our experimental conditions. Here we tested the effect of elliptical elements on perceptual organization by testing their effect on perception of global orientation in the grouping task. These effects are compared with effects due to magnification, which affect inter-element proximity, and are expected to introduce an opposite bias in perception. Here we confirm that perception is based on spatial integration (i.e., global) by comparing performance with stimuli of different sizes, and we quantify the relationship between the two factors affecting perceived global orientation – element elongation and proximity.

A.2. Methods

Six naive observers participated in these experiments; their ages ranged from 25 to 35, and all had normal or corrected-to-normal visual acuity. The same experimental setup as in the main manuscript was used. The monitor resolution was 2048 × 1536 pixels and the viewing distance was 2 m. There were three experimental conditions:

A.2.1. A matrix of four white ellipses presented on a gray background

Each dot diameter was 40 pixels (10.7 min of arc); the distance between the ellipse centers was 200 pixels along the vertical and the horizontal axes. The experimental variable was the ellipse shape, which was either round or was elongated in either the vertical or the horizontal direction by 5%, 10%, or 15% (1, 2, or 3 pixels at each side), resulting in seven different width ratios (1.15, 1.1, 1.05, 1, 0.95, 0.9 and 0.87; Fig. A1A). The task was to report whether the pattern is grouped into horizontal rows or vertical columns. The observer responded by pressing the mouse buttons: right for columns and left for rows. It is important to note that the ellipse centers remained at the same location for all the seven ratios.

A.2.2. A matrix of 16 white ellipses presented on a gray background

Similar to (1) with one exception: the matrix was composed of a 4 × 4 matrix of ellipses, a total of 16 (Fig. A1B).

A.2.3. A matrix of 16 white round dots presented on a gray background

Under this condition the shape of the dots in the 4 × 4 matrix was circular. The spacing between the dots was reduced in the vertical or the horizontal direction by 12, 24, or 36 pixels, and the spacing ratios between the dots matrix were 0.82, 0.88, 0.94, 1, 1.06, 1.13, and 1.21 (Fig. A1D).

The appearance of the margins of the matrix was in most of the conditions rectangular in most cases, due to the unequal spacing between the rows and columns, which may have interfered with the observers' judgment. To avoid such interference, the screen was covered with a round window with a radius of 7.5 cm, so that the global form of the stimulus was circular across all experiments, occupying 5.4 deg of the visual field.

Data were collected for the seven conditions, intermixed (40 trials per datum point), resulting in a run of 280 trials that lasted from 9 to 11 min. Each trial was preceded by a fixation mark at the center of the display until the observer signaled his readiness using the middle button of the computer mouse. Then a stimulus was briefly presented for 80 ms and the observer responded, with no feedback.

A.3. Results

Perceptual grouping determines whether the spatial arrangement of a dot matrix is perceived as columns or rows. A psychometric curve was obtained for each observer and then the

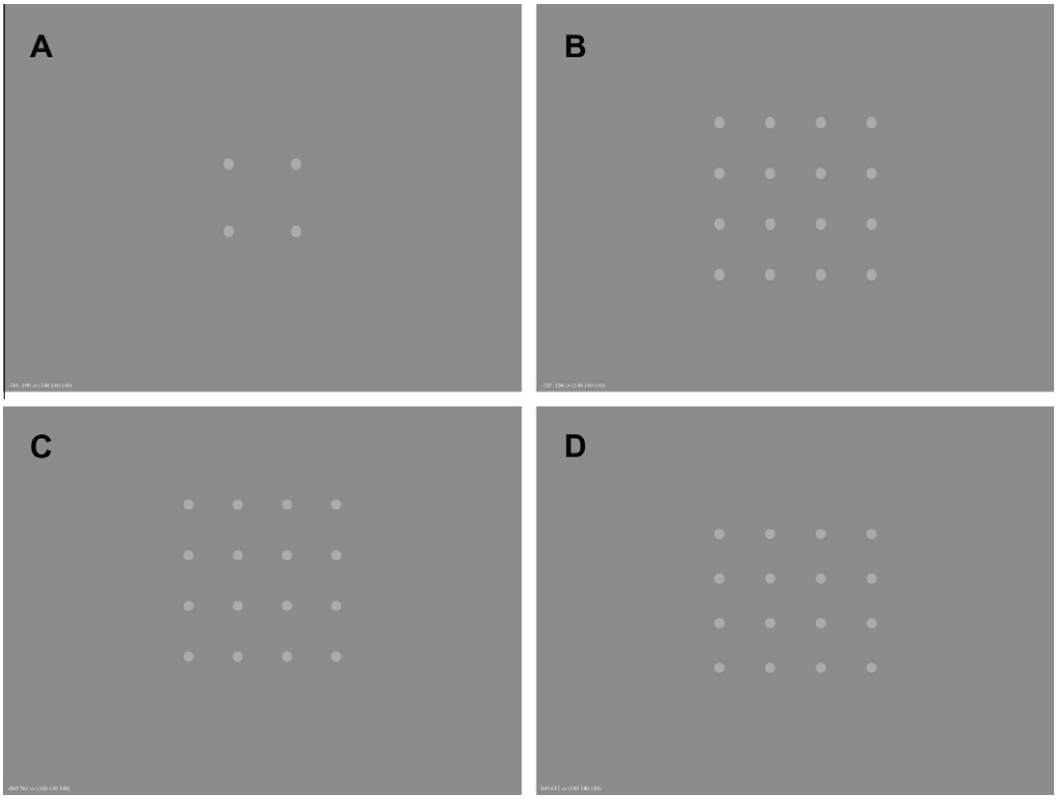

Fig. A1. Stimuli examples. The extreme cases (the highest ratio between the vertical vs. the horizontal gaps) for (A) a 4-ellipse matrix, (B) a 16-ellipse matrix, (C) a 16-dot matrix with smaller or (D) larger spacings.

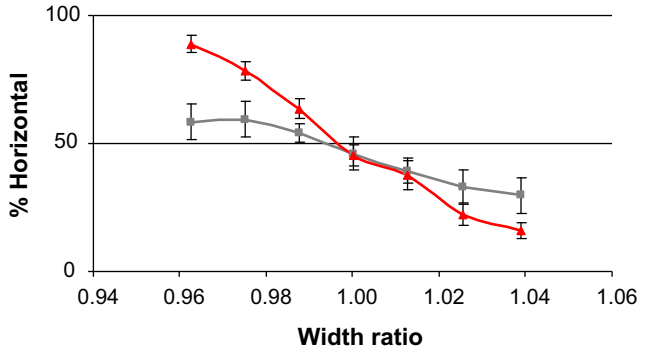

Fig. A2. Ellipse matrix of 4 vs. 16 elements (conditions 1 and 2). The *y*-axis represents the percentage of the correct horizontal answers. The *x*-axis represents the ratio between the vertical vs. the horizontal dimensions of the ellipses (width ratio). The distances between the ellipse centers remained unchanged at 200 pixels. The effect on perceptual grouping was much more pronounced in the matrix composed of 16 ellipses (red triangles) compared with the 4-ellipse matrix (gray squares). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

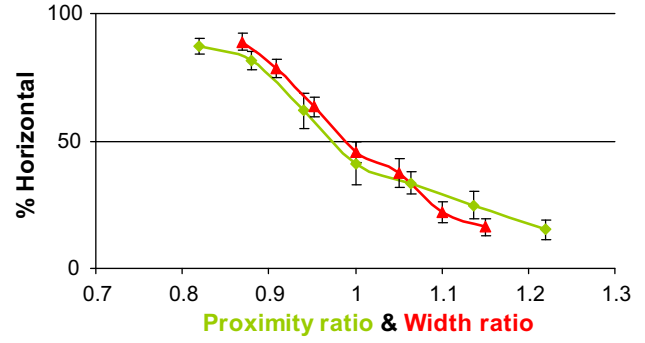

Fig. A3. 16-Element matrices with different width and spacing ratios. The results from Fig. 2 with the same spacing ratios (a matrix composed of 16 ellipses (red triangles)) are compared with the 16-dot matrix with equivalent spacing ratios (green diamonds). The *x*-axis represents the spacing ratio for the dot matrix and the width ratio for the ellipse matrix. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

average for the group was calculated. The percentage of horizontal judgments (reported as rows) is plotted separately for each ratio.

Fig. A2 compares the results of the 4-ellipse matrix (condition 1) with the 16-ellipse matrix (condition 2). The grouping was significantly more accurate for the 16-ellipse matrix compared with the 4-ellipse matrix ($p < 0.001$, paired *t*-test). The slope of the 16-ellipse matrix was much steeper than that of the 4-ellipse matrix (-2.55 and -1.09, respectively).

Fig. A3 compares the results of the 16-element matrices composed of ellipses (condition 2) vs. dots (condition 3a) using a common abscissa, a shape ratio for the ellipses and a spacing ratio for circles. As can be clearly seen, the two curves are very similar ($p = 0.87$, paired *t*-test), implying a quantitative equivalence between effects due to spacing and shape biases, as expected from the autocorrelation model of perceptual grouping (Ben-Av and Sagi, 1995).

A.4. Conclusion

The results show that, for our stimuli, (1) perceptual grouping results from spatial integration over display elements, not a local effect, and (2) a quantitative agreement exists between shape-dependent and space-dependent biases in grouping. When considering a lens of +1.00 D, which produces a blur-induced shape bias equivalent to a width factor of $\sim$2 and an elongation of $\sim$1.01, we expect the blur effect to dominate.

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